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Native anuran species as prey of invasive American Bullfrog, *Lithobates catesbeianus*, in Brazil: a review with new predation records

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***Abstract.*—The American Bullfrog (*Lithobates catesbeianus*) is widely distributed throughout the world as an invasive species, and causes negative impacts on the fauna resulting from its voracious predatory activity. This study documents two new predation reports and reviews the previous predation reports of the American Bullfrog on native Brazilian anurans. Twenty-one species of native anurans were recorded as American Bullfrog prey in Brazil. A positive correlation was found between the number of native anurans preyed on by American Bullfrog and the respective family or number of species per genus. Most of the prey species are small or medium-sized, and the results suggest that the generalist diet and intraguild predation may have favored the widespread establishment of the American Bullfrog.**

Keywords. Amphibia, Atlantic Forest, biological invasion, conservation, global change, intraguild predation, exotic species

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Introduction

Biological invasions represent a major threat to natural ecosystems and their respective biodiversity, human health, and food security (IUCN 2012). In this context, the American Bullfrog, *Lithobates catesbeianus* (Shaw, 1802), is a globally widespread introduced species (Lowe et al. 2004). It is native in North America, occurring from eastern Canada and the central and eastern United States to northeastern Mexico (Quiroga et al. 2015). The introduction of *L. catesbeianus* in non-native environments has direct (e.g., predation and competition) and indirect (e.g., parasites, disease introduction, and biotic homogenization) impacts on biodiversity (Batista 2002; Batista et al. 2015; Kiesecker and Blaustein 1998; Kraus 2009).

Lithobates catesbeianus is a voracious predator whose diet includes a wide variety of prey (Boelter and Cechin 2007; Boelter et al. 2012; Silva et al. 2009). Juveniles feed mainly on insects (Silva et al. 2009), whereas adults prey upon invertebrates and small vertebrates, such as fish, reptiles, birds, and mammals (Quiroga et al. 2015).

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American Bullfrogs are considered opportunistic feeders, also preying on amphibians, including conspecifics and other species (Silva et al. 2011; Toledo et al. 2007).

The American Bullfrog is now established in nearly 40 countries around the world (Frost 2019; Kraus 2009). In Brazil, the first specimens were introduced in 1935 for commercial exploitation at the municipality of Itaguaí, Rio de Janeiro state (Vizotto 1984). The introduction of the American Bullfrog for commercial frog farming was due to its fast reproduction and greater development in captivity compared to native species. It occurs mainly in the southern and southeastern Brazilian states because of its easy adaptation to the climatic conditions (Vizotto 1984). Approximately 2,000 commercial frog farms were active in the early 1990s in Brazil, but many closed their activities because of low profitability (Lima and Agostinho 1988), which led to American Bullfrog specimens being abandoned or released into the natural environments, and consequently several accidental invasions have occured in Brazil (Both et al. 2011).

Populations of *Lithobates catesbeianus* are now known to be present in 155 Brazilian municipalities (Both et al. 2011; Instituto Horus 2016), a context in which many studies have revealed the localized impacts of its predatory activity on native anuran fauna (Batista et al. 2015; Boelter and Cechin 2007; Boelter et al. 2012; Leivas et al. 2012; Silva et al. 2011). In addition, global-scale studies have demonstrated trophic niche-width shifts in bullfrog populations from both native and invaded areas (Bissattini and Vignoli 2017), as well as the effects of the interactions between bullfrogs and crayfish on native amphibians (Bissattini et al. 2018, 2019; Liu et al. 2018). However, studies summarizing data on the predation of native anurans by American Bullfrogs have yet to be presented; therefore, knowledge on the impact and the native anuran species preyed upon by such an invasive frog may benefit our understanding of their predator-prey relationships.

Herein, the predation of *Boana raniceps* and *Phyllomedusa distincta* by males of *Lithobates catesbeianus* are reported, and the available literature on the predation of native anurans by the invasive frog *L. catesbeianus* in Brazil is reviewed. An overview on the number and identities of native species reported as prey and the potential impact of the American Bullfrog on native anurans are provided.

Material and Methods

Bibliographic Review

An extensive literature review was conducted to find scientific articles, natural history notes, and theses which contain reports on the predation of native anurans by the invasive American Bullfrog *Lithobates catesbeianus* in Brazil. The sources included articles or natural history notes published in *Herpetological Review* (1967–2018), *Herpetological Bulletin* (2008–2018), *Herpetology Notes* (2008–2018), and *South American Journal of Herpetology* (2006–2018). Searches were also conducted in Web of Science using the following query: ("*Rana catesbeiana*" OR "*Lithobates catesbeianus*") AND ("diet" OR "feeding biology" OR "predation"), applied in the field "topic" on 30 December 2018, without applying any filters for year or other parameters. Considering that predation attempts would not necessarily result in a predation event (Toledo et al. 2007), reports of predation attempts in the field, laboratory experiments, or captivity were not included. Masters and doctoral papers in digital format were obtained from the library databases of Brazilian universities (especially Universidade Estadual Paulista and Universidade Regional de Blumenau) by using the search terms mentioned above in the Google search engine.

The Web of Science query resulted in 159 studies, three of which met the criteria and were included in the study. Eight additional predation records were selected for inclusion in the study by searching the selected journals (six studies) and the library databases of Brazilian universities (two studies). Information was extracted from each diet analysis (i.e., the diet was described through the analyses of stomach contents or predation records), study location, anuran prey species, geographic range, and body size. The geographic range follows the list of anuran species for each Brazilian federal state and the biomes proposed in Toledo and Batista (2012). The body sizes of anuran species follow the size values available in Uetanabaro et al. (2008) and Haddad et al. (2013). The spatial distribution map of *Lithobates catesbeianus* invasive populations and predation reports were generated with 155 occurrence points for American Bullfrog in Brazil, obtained from Both et al. (2011) and Instituto Horus (2016).

Data Analysis

The relation between the number of native anuran species preyed upon by the American Bullfrog and the number of native anurans per family or genus was tested with a Pearson correlation analysis. The numbers of native anuran prey species per family and genus were compiled following the Frost (2019) database. Toledo et al. (2007) stated that a positive correlation between the number of predation events and taxonomic richness may be a proxy for search representativeness, by reasoning that taxa with more species would be more frequently predated by chance (i.e., a sampling effect). Such a correlation could indicate the possible mechanisms of *L. catesbeianus* impacts on native biota apart from search representativeness.

Fig. 1. Adult *Lithobates catesbeianus* swallowing an adult *Boana raniceps* in an artificial permanent pond within pasture area in southern Brazil.

Results

Field Observations and New Predation Records

An adult *Lithobates catesbeianus* swallowing an adult *Boana raniceps* (Fig. 1) was recorded on 11 October 2014 at 2100 h, in an artificial permanent pond inside a pasture area (23º20'38"S, 51º52'07"W), in the northern region of Paraná state, southern Brazil. Although the specimens escaped, voucher specimens of the native anuran species and *L. catesbeianus* had been previously collected by Affonso et al. (2014) and stored at the Amphibian Collection from the Zoology and Botany Department, Bioscience Institute, Universidade Estadual Paulista, Rio Claro, São Paulo, Brazil.

A second predation event recorded a male adult specimen of Bullfrog swallowing a treefrog (Fig. 2A). The specimen was collected during an *L. catesbeianus* survey on 22 January 2019, at 2200 h, in an artificial permanent pond in a rural property at Iporanga, southern São Paulo state, southeastern Brazil (24º35'01.2"S, 48º36'00.4"W). The *L. catesbeianus* specimen was taken to the laboratory where the anuran prey was removed and identified as an adult *Phyllomedusa distincta* (Fig. 2B).

Exploratory Analysis

Overall, 11 publications reported predation events, corresponding to 41 records of native anurans as prey of *L. catesbeianus* (Table 1). Nine of the publications discussed the diet in a broader sense, and two were natural history notes reporting predation events. Most of the records occurred in Minas Gerais state (39%), followed by Rio Grande do Sul (~32%), Paraná (~12%), São Paulo (~12%), and Santa Catarina (~5%), at sites inside the Atlantic Forest, in addition to another site in a transition zone between Cerrado and Atlantic Forest (Fig. 3, Table 1).

This survey accounted for 21 anuran species as prey of *L. catesbeianus*, all widely distributed and possibly coexisting with American Bullfrogs in their breeding sites. The anuran family Hylidae had the highest number of species (11 species), followed by Leptodactylidae (four species), Bufonidae and Microhylidae with two species each, and Odontophrynidae and Phyllomedusidae with one species each. *Lithobates catesbeianus* often preyed on medium-sized species, but small-sized species were also preyed upon (Table 1).

A positive correlation was found between the number of native anuran species preyed on by American Bullfrog and genus richness ($r = 0.71$, $P = 0.01$), whereas at the family level no relationship was found ($r = 0.53$, $P = 0.22$). Thus, considering the studies analyzed, genera with higher numbers of species presented more potential prey for American Bullfrogs in Brazil.

Discussion

Most of the predation records found in this review came from a few studies which assessed the overall dietary composition of *L. catesbeianus*, and revealed that the diet of these invasive frog populations is represented by a wide variety of native anuran species (Boelter and Cechin 2007; Silva et al. 2009, 2010, 2011). Only two predation records of *L. catesbeianus* and native anurans in the field were found, probably due to some difficulty

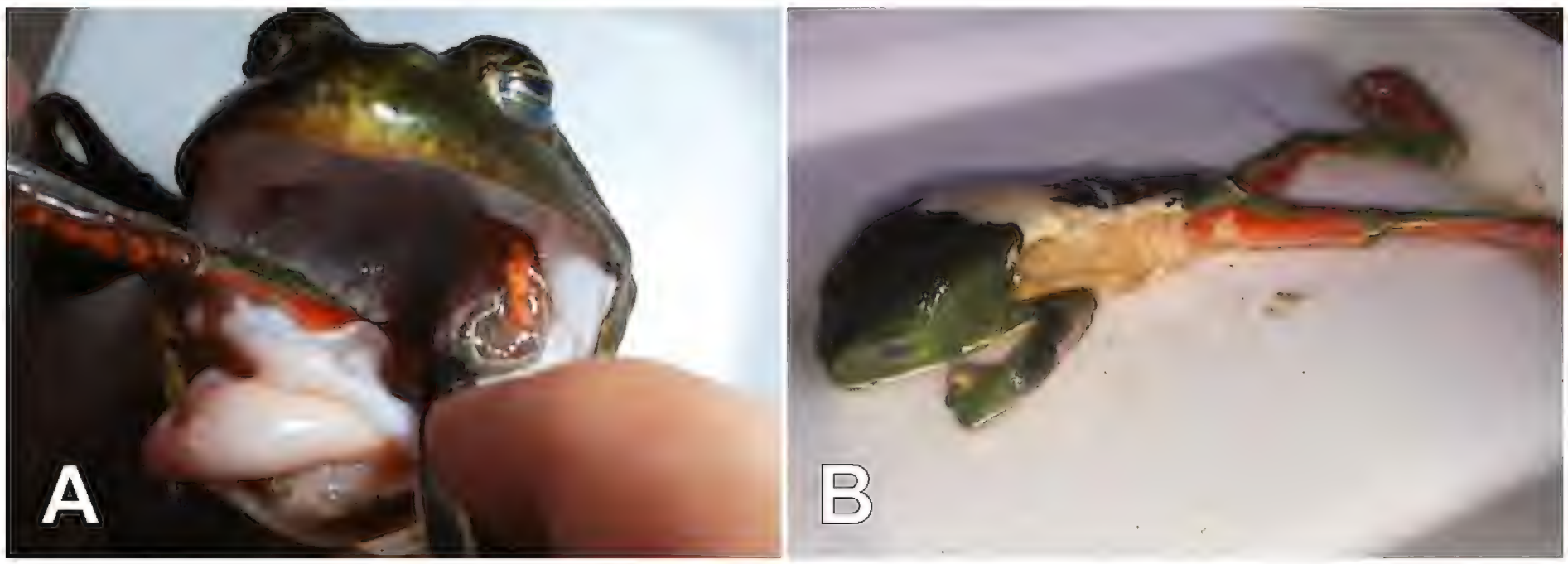

Fig. 2. (A) Predation of an adult *Phyllomedusa distincta* by *Lithobates catesbeianus*, **(B)** Adult *P. distincta* partially digested, removed from the oral cavity of *L. catesbeianus*.

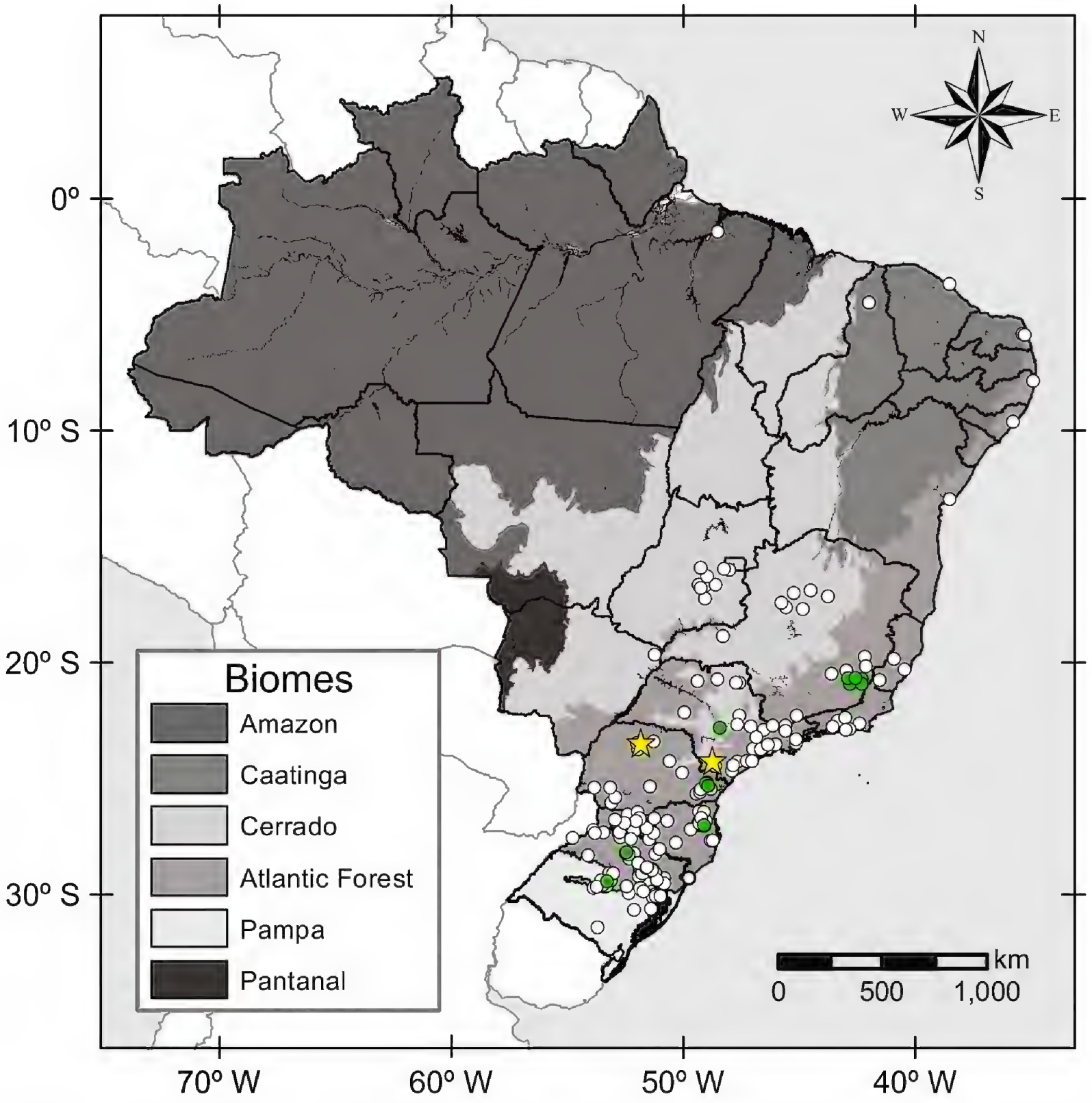

Fig. 3. Spatial distribution of *Lithobates catesbeianus* invasive populations and predation reports of native anurans in Brazil. White circles: American Bullfrog populations in Brazil (Both et al. 2011; Instituto Horus 2016); yellow stars: predation reports of adult *Boana raniceps* and adult *Phyllomedusa distincta* in southern and southeastern Brazil; light green circles: locations of 41 published predation records.

in recording and quantifying these events in the field (Pombal Jr. 2007).

The predicted potential occurrence of *L. catesbeianus* in Brazil represents its current distribution in the southern and southeastern regions in the Atlantic Forest, with potential areas for colonization remaining in the central and northeastern regions (Giovanelli et al. 2008; Both et al. 2011). The results showed that all predation records occurred at sites in southern and southeastern Brazil, regions with higher numbers of research centers, thus contributing a disproportionately greater number of field studies.

Native anurans recorded as prey of American Bullfrogs share the same breeding sites. Silva et al. (2011) had found a spatial overlap in microhabitat use between native species and American Bullfrogs during the reproductive season. American Bullfrogs may also overlap with native amphibians in diet composition (Bissattini et al. 2019). This may lead to a potential competition, and may have a direct influence on community composition patterns since the intrinsic ecological properties of organisms determine the niche overlap between species in the communities (Vignoli and Luiselli 2012; Vignoli et al. 2017). Additionally, the predation on other anuran species by *L. catesbeianus* can represent an example of intraguild predation (Polis et al. 1989), a process that may facilitate the establishment of the American Bullfrog (Bissattini et al. 2018), as found in other disparate introduced taxa, such as ladybird beetles (Snyder et al. 2004) and fish (Pereira et al. 2015). Intraguild predation can benefit the establishment of *L. catesbeianus* by reducing the competitive pressure by direct predation of the other anuran species.

The number of prey species had a positive correlation with the number of species per genus, in which the family Hylidae had the highest number of species as

Table 1. Native anuran species as prey of *Lithobates catesbeianus* in Brazil based on 41 records obtained from 11 publications, and from two predation events reported here from southern and southeastern Brazil.

Anuran prey species	Body Size[a] (cm)		Locality[b]	Biomes[c]	Reference
	SVL ♂	SVL ♀			
Bufonidae					
Rhinella abei (Baldissera-Jr, Caramaschi and Haddad, 2004)	6.1	9.3	Quatro Barras, Campina Grande do Sul, and Bocaiúva do Sul, PR	AF	Leivas et al. 2012
Rhinella ornata (Spix, 1824)	6.4	7.9	Viçosa, MG	AF, Ce	Reis et al. 2007
			Viçosa, MG		Silva et al. 2010
Hylidae					
Dendropsophus elegans (Wied-Neuwied, 1824)	2.9	3.1	Viçosa, MG	AF, Ca	Silva et al. 2009
			Viçosa, MG		Silva et al. 2011
			Viçosa, MG		Silva et al. 2016
Dendropsophus minutus (Peters, 1872)	2.3	2.5	Agudo and Nova Palma, RS	AF, Am, Ca, Ce, Pt, Pp	Boelter and Cechin 2007
			Agudo and Nova Palma, RS		Boelter et al. 2012
			Viçosa, MG		Silva et al. 2009
			Botucatu, SP		Almeida 2010
Dendropsophus nanus (Boulenger, 1889)	2.0	2.3	Botucatu, SP	AF, Am, Ca, Ce, Pt, Pp	Almeida 2010
Boana albomarginata (Spix, 1824)	5.1	5.8	Blumenau, SC	AF, Ca, Ce	Dallacorte 2010
Boana bischoffi (Boulenger, 1887)	4.5	5.9	Quatro Barras, Campina Grande do Sul, and Bocaiúva do Sul, PR	AF, Ce, Pp	Leivas et al. 2012
Boana faber (Wied-Neuwied, 1821)	8.8	8.9	Viçosa, MG	AF, Ca, ce	Silva et al. 2009
			Blumenau, SC		Dallacorte 2010
Boana pulchella (Duméril and Bibron, 1841)	4.2	4.5	Agudo and Nova Palma, RS	AF, Pp	Boelter and Cechin 2007
			Agudo and Nova Palma, RS		Boelter et al. 2012
Boana raniceps Cope, 1862	7.1	6.8	Maringá, PR	AF, Am, Ca, Ce, Pt	This sudy
Scinax crospedospilus (A. Lutz, 1925)	3.0	3.1	Viçosa, MG	AF	Silva et al. 2009
Scinax eurydice (Bokermann, 1968)	5.3	4.8	Viçosa, MG	AF, Am, Ca, Ce	Silva et al. 2009
			Agudo and Nova Palma, RS		Boelter and Cechin 2007
			Agudo and Nova Palma, RS		Boelter et al. 2012
Scinax fuscovarius (A. Lutz, 1925)	4.2	4.5	Botucatu, SP	AF	Almeida 2010
			Viçosa, MG		Silva et al. 2010
			Vieiras, MG		Silva et al. 2011
			Vieiras, MG		Silva et al. 2016

Table 1 (continued). Native anuran species as prey of *Lithobates catesbeianus* in Brazil based on 41 records obtained from 11 publications, and from two predation events reported here from southern and southeastern Brazil.

Anuran prey species	Body Size[a] (cm)		Locality[b]	Biomes[c]	Reference
	SVL ♂	SVL ♀			
Leptodactylidae					
Leptodactylus fuscus (Schneider, 1799)	4.4	4.4	Agudo, and Nova Palma, RS	AF, Am, Ca, Ce, Pp, Pt	Boelter and Cechin 2007
			Agudo, and Nova Palma, RS		Boelter et al. 2012
Leptodactylus latrans (Steffen, 1815)	9.6	9.2	Quatro Barras, Campina Grande do Sul, and Bocaiúva do Sul, PR	AF, Am, Ca, Ce, Pp, Pt	Leivas et al. 2012
Physalaemus cuvieri Fitzinger, 1826	2.8	3.1	Agudo and Nova Palma, RS	AF, Am, Ca, Ce, Pp, Pt	Boelter and Cechin 2007
			Agudo and Nova Palma, RS		Boelter et al. 2012
			Botucatu, SP		Almeida 2010
			Quatro Barras, Campina Grande do Sul, and Bocaiúva do Sul, PR		Leivas et al. 2012
Pseudopaludicola mystacalis (Cope, 1887)	1.7	2.1	Vieiras, MG	AF, Am, Ca, Ce, Pp, Pt	Silva et al. 2011
			Vieiras, MG		Silva et al. 2016
Microhylidae					
Elachistocleis cesarii (Miranda-Ribeiro, 1920)	2.9	3.2	Vieiras, MG	AF, Ca, Ce	Silva et al. 2011
			Vieiras, MG		Silva et al. 2016
Elachistocleis bicolor (Guérin-Menéville, 1838)	2.8	3.8	Agudo and Nova Palma, RS	AF, Ce, Pp	Boelter et al. 2012
Odontophrynidae					
Odontophrynus americanus (Duméril and Bibron, 1841)	4.5	4.9	Agudo and Nova Palma, RS	AF, Ca, Ce, Pp	Boelter and Cechin 2007
			Passo Fundo, RS		Leivas et al. 2013
Phyllomedusidae					
Phyllomedusa distincta Lutz, 1950	5.6	6.0	Iporanga, SP	AF, Ce, Pp	This study

[a] Values of snout-vent length (SVL) available in Uetanabaro et al. (2008) and Haddad et al. (2013).

[b] Brazilian states: MG = Minas Gerais; PR = Paraná; RS = Rio Grande do Sul; SC = Santa Catarina; SP = São Paulo.

[c] Occurrence of anuran species within Brazilian biomes: AF = Atlantic Forest; Am = Amazon; Ca = Caatinga; Ce = Cerrado; Pp = Pampa; Pt = Pantanal.

prey of *L. catesbeianus*. Boelter et al. (2012) found that 60% of the prey records corresponded to Hylidae species, suggesting that this group suffers higher predation pressure. At least two non-mutually exclusive hypotheses may explain these patterns by relating family (i.e., richness, abundance) and species traits (i.e., body size) to *L. catesbeianus* predation rates, involving species traits that are often phylogenetically correlated (Martins and Hansen 1997). Firstly, it is possible that Hylidae species are often preyed upon due to their higher species richness in comparison to other families, which is a plausible hypothesis if we assume that predation rates can be proportional to prey abundance or richness (i.e., higher predation rates in higher resource availability conditions; Jacobsen et al. 2014; Madahi et al. 2015). Secondly, Hylidae species may have a higher predation rate because of their smaller size relative to species from other families (e.g., Bufonidae). Predators that feed on whole animals, such as the American Bullfrog, are limited by the prey's body size. Experimental evidence indicates that larger specimens of *L. catesbeianus* feed preferentially on smaller, rather than on large-sized, native anurans (Wang et al. 2007), suggesting a size-based selection of prey species. Partially related to this hypothesis, our results suggest a higher amount of small and medium-sized species as American Bullfrog prey. Therefore, the preference for prey of a certain body size may be proportionally related to the body size of the predators, as observed in previous studies (Quiroga et al. 2015; Silva et al. 2011, 2009; Wang et al. 2007).

This survey found that all anuran species preyed upon by *L. catesbeianus* have large geographic distributions, occurring in various Brazilian states and biomes (Frost 2019; Toledo and Batista 2012). Both et al. (2014) found that American Bullfrog abundance had a positive relationship with communities that consisted of generalist species (e.g., *Physalaemus cuvieri*, *Dendropsophus minutus*), that were anthropogenically adapted and broadly distributed in South America. Native anurans with large geographic ranges (e.g., *Rhinella diptycha*, *Dendropsophus minutus*, *Boana faber*, *B. raniceps*, *Scinax fuscovarius,* and *Physalaemus cuvieri*) have also been found in sympatry with *Lithobates catesbeianus* elsewhere (Affonso et al. 2014).

Conclusions

This study indicated *L. catesbeianus* preys on at least 21 native anuran species in Brazil. Predation is one of the major negative effects of invasive species on native communities. The quality of being a generalist feeder, preying on many anuran species, has benefited the successful colonization, establishment, and permanence of the American Bullfrog in Brazil (and even worldwide; e.g., Li et al. 2011; Monello et al. 2006; Quiroga et al. 2015). Native species of the family Hylidae may be more susceptible to American Bullfrog predation because of their higher abundance and richness, and/or due to a higher representation of small- to medium-sized species relative to other anuran families. Knowledge on the species most vulnerable to predation by the American Bullfrog can enable better prediction of the negative impacts of such an invasive species on native anuran communities.

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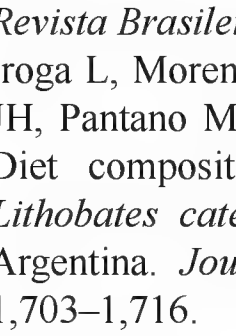

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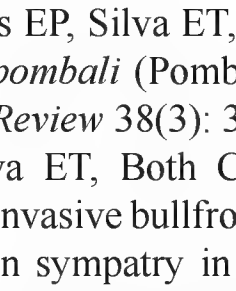

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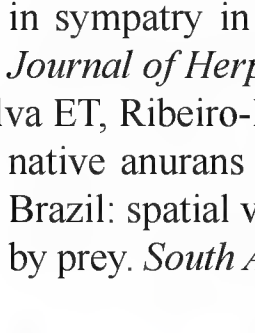

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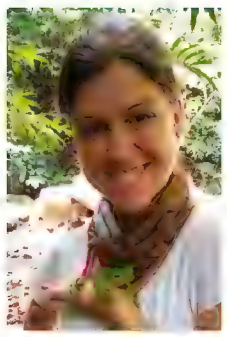

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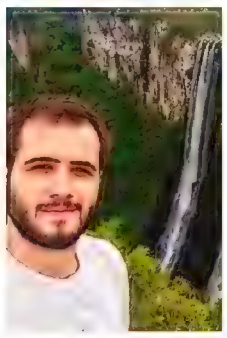

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